Effects of refuge availability on growth and survival of YOY Arctic char (*Salvelinus alpinus*)

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Abstract

Risk of predation induces behavioural responses in prey, such as decreased activity and avoidance of risky habitats. Sheltering by prey in low risk habitat not only constrains the physical area but also the accessibility of resources. Hence, variation in refuge availability affects the performance of refuging individuals. In a large scaled pond experiment I tested the effect of refuge availability on survival and growth in young-of-the-year (YOY) arctic char (*Salvelinus alpinus*), subject to predation from cannibalistic char. In addition, I also studied the behaviour of YOY char in response to predation risk. Results showed that predation decreased both survival and growth of YOY char. Increasing refuge availability decreased the mortality of YOY char, but had no effect on growth. Risk of predation restricted the habitat use of YOY char to the protected near shore habitat. There was also a density dependent resource depletion in the refuge habitat when cannibals were present, induced by refuge availability and habitat use of YOY char. The overall results suggest predation to be the key factor limiting growth and survival in YOY char rather than resource competition, and that both quality and density of refuges affect the survival of YOY char.

Introduction

Predation is a key structuring force affecting population and community dynamics. First by the direct numerical decrease of individuals in prey populations, which in turn may decrease resource competition between prey. Secondly, through the indirect effect of a variety of behavioural responses by prey to avoid predation that ultimately affects the fitness of individual prey. In order to assess the consequences of predation at the population level, understanding the individual level responses to avoid predation then becomes of major importance (Huang and Sih 1991, Werner and Anholt 1996, Beckerman et al. 1997). For example, individuals have been shown to reduce their activity to avoid predation at the cost of reduced growth (Sih 1982, Werner and Gilliam 1984, Lima and Dill 1990, Houston et al. 1993, Werner and Anholt 1993).

Littoral areas are due to their structural complexity considered to be low risk habitats for small fish, compared to the high risk area of open pelagic water where there are less physical refuges from piscivorous fish (Werner and Hall 1988, Turner and Mittelbach 1990). Evidence is immense that individuals utilize the structural complex habitats like the littoral zone to escape predation (Werner and Hall 1988, Persson 1993, Eklöv and Diehl 1994, Eklöv and Persson 1995, Persson and Eklöv 1995, Byström et al. 2003, Biro et al. 2003a). For example, Biro et al. 2003b shows that decreased activity and avoidance of risky habitats mediates higher survival in young fish at the whole-system scale. However, high densities of refuging prey may cause density dependent resource depletion in refuge habitats, and consequently decrease growth rates of refuging individuals.

In this study I examined the effects of increasing refuge availability and predation on the growth and mortality of YOY arctic char (*Salvelinus alpinus*). As predators I used large cannibalistic char. Refuge density were varied by adding additional artificial refuges to the natural near shore vegetation at two different densities, creating a refuge gradient between treatments. First, I hypothesized that mortality would decrease with increasing availability of refuges. Secondly, growth rates would be higher in the absence of predation risk as YOY char can exploit all available resources. Third, growth rate in the presence of predation risk should increase with increasing refuge availability, as density dependent effects in refuge areas in fish decreases with increasing habitat (refuge) size. Finally, resource densities close to refuges should be lower compared to the open water due to strong exploitation of refuge resources.

Material and methods

Experimental design

I conducted a large scale pond experiment to examine the effects of cannibalism on growth and mortality responses of YOY arctic char in a refuge gradient. The experiment was carried out in two artificial ponds (32 x 10.8m, mean depth 0.90m) in Umeå, during 15 days in mid June 2003. Both of the ponds were divided with reinforced dark green plastic sheets, across their width, into eight enclosures (4 x 10.8m) (Fig. 1). Enclosures had separate water inlets and were connected to water outlets, located in enclosures 8 and 16, through fine mesh (3mm) openings in the enclosure walls. The littoral zone of each enclosure measured two times four meters, except for enclosures 1, 8, 9 and 16 which had an additional 10.8m of littoral zone. Prior to the start of the experiment vegetation outside the shoreline in the ponds was cleared out, to make them as equal as possible in respect to structural complexity. Nonetheless, vegetation belts formed during the experiment at varying densities in the enclosures, and the main difference in vegetation coverage was between the two ponds. For a more detailed description of the ponds see Byström and Andersson (2005).

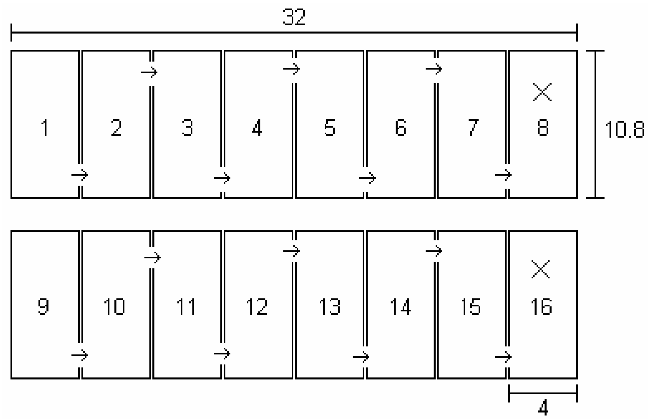

Figure 1. Schematical drawing of the two experimental ponds with eight enclosures each. Numbers inside each enclosure stands for enclosure number and numbers next to lines notes distance in meters. Water inlet were located in the centre of each enclosure, arrows note direction of water flow between the enclosures. X denotes point of water outlet.

To examine the effects of refuge availability on YOY char performance, the experimental design had three different refuge treatments with four replicates in each, equally divided between the two ponds. To vary the availability of refuge between the treatments, units of artificial refuges were used. These were constructed from plastic crates (39 x 25 x 27 cm), and plastic plant containers (38 x 38 x 7 cm). The refuge was built up by subunits of one crate and one plant box, subunits were then linked together to get the desired amount of refuge for each treatment. Refuge units were then submerged in the littoral zone on both sides of each enclosure, with approximately five centimetres of water above the top of the refuge. Densities of refuge were denoted as low for natural refuge habitat, intermediate for two meters of additional artificial refuge and high for four meters of additional artificial refuge on each side of the enclosures. To evaluate the survival and performance of YOY char in the absence of predation, each pond had a control treatment without cannibals with a refuge density corresponding to that of the intermediate treatment.

Fish

Two cannibals, mean length (± 1 SD) 242.75 ± 19.3 mm and mean weight (± 1 SD) 130.57 ± 36.0 g, were acclimatized in each enclosure 20 days prior to the introduction of YOY char. Cannibals had been kept in a neighbouring pond over winter stocked with small char, and were documented to be potential cannibals as attacks on YOY-char were observed in all enclosures within a few minutes after introduction of YOY char. Each enclosure was stocked

9th of June with 100 hatchery reared YOY-char originating from wild parents. Mean initial length (± 1 SD) and weight (± 1 SD) of the introduced YOY char were 44,72 ± 3,69 mm and 0,596 ± 0,17 g (N = 104) respectively. Introduction of YOY char was done by gently releasing half of the individuals into the refuge areas on each side of the enclosures.

On three occasions; at the beginning, in the middle and at the end of the experiment, behaviour of both cannibals and victims were studied. Each enclosure was studied for ten minutes while noting the positions of YOY-char at two minutes interval, giving a total of five measurements per occasion. Cannibal activity was studied continuously during the ten minute period of observation, concluding that activity differed little between enclosures and that cannibals occupied mainly the deeper habitat outside the refuge areas.

Fish were captured at the end of the experiment (June 23rd) with a seine net. Sampling was performed in each enclosure until three subsequent empty sampling efforts were reached. Captured fish were stored on ice for later weight and length measurements in laboratory. For each enclosure, stomachs from ten individuals were removed and preserved in alcohol for later diet analysis. For the stomach analysis both zooplankton and macro invertebrates were classified to order, family or genus. Length of ten individuals for each zooplankton taxa were measured for conversion into dry weights with regressions relating body length to dry weight (Dumont et al. 1975, Bottrell et al. 1976). Length or head width for all ingested macro invertebrate taxa were measured for conversion into dry weight (Persson et al. 1996). Total dry weights of each prey category were then used to estimate the proportion of each prey in YOY char diet.

Resources

Macro invertebrates were sampled at the start and at the end of the experiment. In this report only final densities are presented. Samplings were done in the area where the artificial refuges were placed and at similar locations for treatments without additional refuge. Two meters of the bottom substrate were sampled with a net measuring 0.25 meters in width giving a total surface area of 0.5 m^2 sampled. Samples were preserved in ethanol and later stained with Bengal rose. Macro invertebrate fauna was classified to order, family or genus. Fifteen individuals of each invertebrate category were length or width measured for estimates of biomass, using regressions relating body length to dry weight (Persson et al. 1996). To estimate the amount of available resources for YOY char, only invertebrate fauna ranging from the smallest size observed in the diet of char to a maximum size of 110 % of the largest ingested prey item of each prey category were used for calculating resource abundance.

Zooplankton was sampled on three occasions; at the beginning, the middle and at the end of the experiment. Two habitats in each enclosure were sampled, one sample (littoral sample) was taken immediately outside artificial refuges, or at similar locations in treatments without artificial refuges. And a second sample (pelagic sample) was taken in the open water in the middle of each enclosure. For the sampling a zooplankton net with a mesh size of 100 µm (∅ 25 cm) was pulled parallel to the enclosure bank at a speed of approximately 0.4 m/s. For the littoral samples the width of the artificial refuge was sampled, whereas the whole width of the enclosure was sampled in all pelagic samples and in littoral samples with no artificial refuge. Samples were preserved with Lugol´s solution. Zooplankton was then classified to family or genus, and the length of twenty individuals of each taxon was measured. Lengths of zooplankton were transformed to dry weight with regressions relating body length to dry weight (Dumont et al. 1975, Bottrell et al. 1976). The zooplankton resources were divided into two groups, cladocerans and copepodes. The cladoceran group included mainly bosmina and chydorides, and the copepod group consisted of cyclopoid and calanoid copepodes.

Statistical analysis

Proportion data for diet and mortality were arc sin √ transformed, and the natural logarithm (LN) were used for all other transformations to obtain natural distribution of the data. Statistical tests were performed in SPSS software v 12.0.1 for windows, ©SPSS inc., 1989-2003.

Results

Survival and growth

There were no differences in the two major response variables, growth and survival, of YOY char between ponds despite their dissimilarities in vegetation cover (One-way ANOVA, pond effect, growth, $F_{1,6} = 2.90$, $p = 0.14$, survival, $F_{1,6} = 2.70$, $p = 0.15$). Therefore, data for ponds were pooled and only effects of treatments are presented for resources, diets and behaviour.

Both survival and growth of YOY arctic char was negatively affected by the presence of cannibalistic char (One-way ANOVA, treatment effect, growth, $F_{3,6} = 7.05$, $p = 0.022$, survival, $F_{3,6} = 45.01$, $p < 0.001$) (Fig. 2). Testing only for the effect of refuge availability on survival and growth of YOY char (by excluding control treatments), increasing refuge availability affected survival positively but had no effect on growth (ANOVA, treatment effect, survival $F_{2,6} = 7.54$, $p = 0.023$, growth, $F_{2,6} = 0.82$, $p = 0.49$) (Fig. 2). YOY char had lower survival in the low natural refuge treatment than in both intermediate and high refuge treatments (Tukey posthoc test, $p < 0.05$). The difference in developed vegetation cover between enclosures, working as a potentially additional refuge, did not have any effect on survival or growth of YOY char (ANCOVA, using refuge treatment as factor and vegetation cover as covariate, effect of vegetation on survival, $F = 0.68$, $p = 0.80$ and growth, $F = 1.35$, $p = 0.28$).

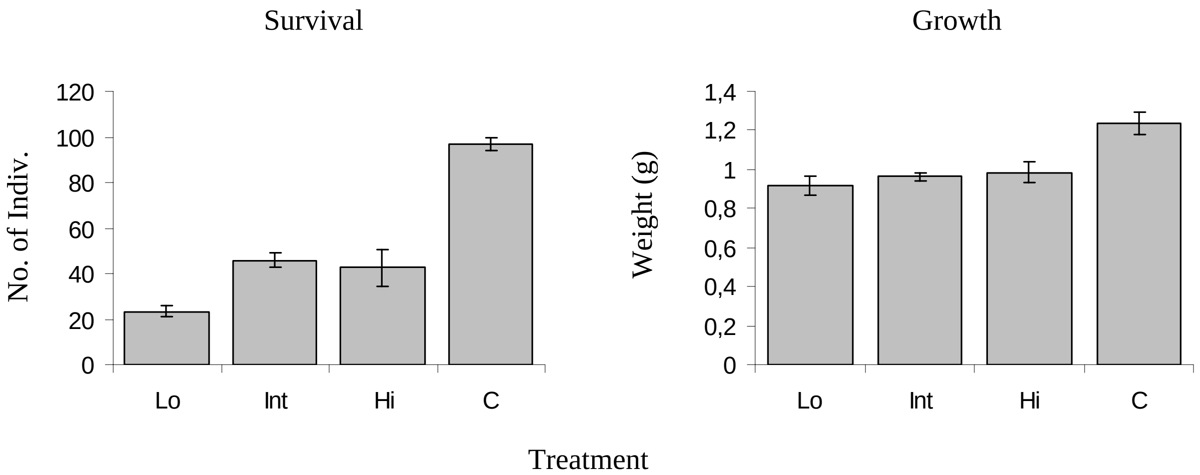

Figure 2. Mean survival and growth (± 1 SE) of YOY char in the different treatments at the end of the experiment.

In addition to differences in growth between treatments with and without cannibalistic char, growth was overall positively related to survival rates in the presence of cannibals (linear regression, $R^2 = 0.38$, $p = 0.03$) (Fig. 3).

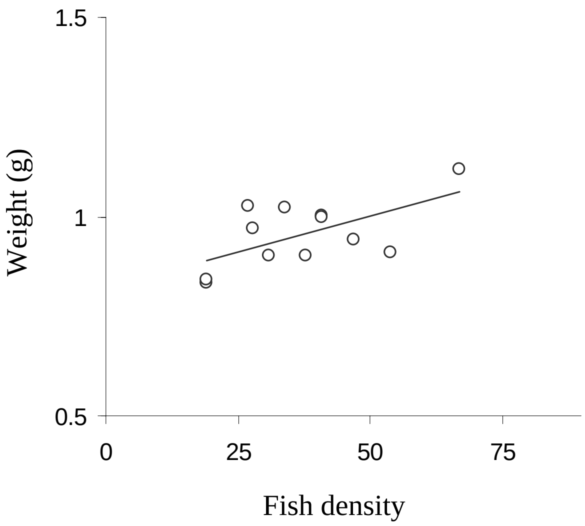

Figure 3. Relation between fish density and weight at the end of the experiment in all enclosures with cannibals.

Diets

The diet of YOY char consisted mainly of macro invertebrates (chironomids and other macro invertebrates, mainly ephemeropterans) and was not affected by the presence of cannibalistic char or by the differing amount of available refuges between treatments (Fig. 4) (Tab. 1).

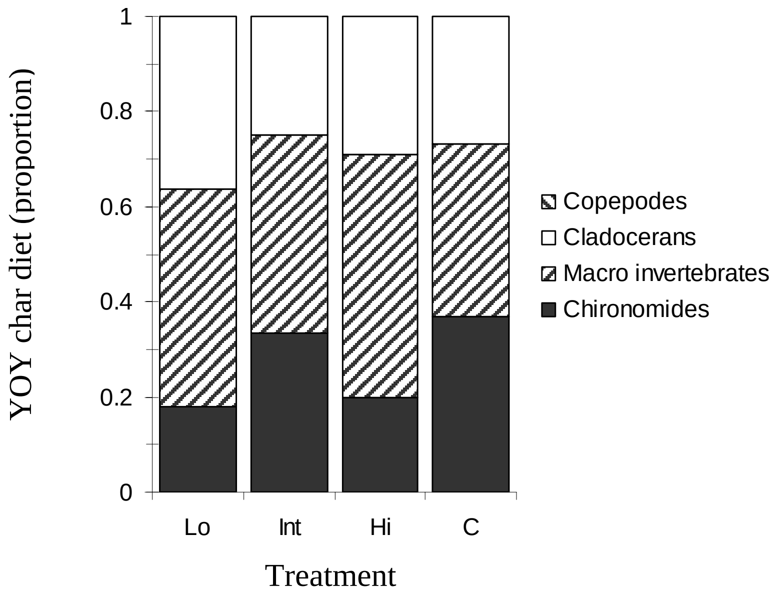

Figure 4. Proportion of prey categories in the diet of YOY char for the different treatments at the end of the experiment.

Table 2. MANOVA (F-values) of the effect of treatment on diet of YOY char and the following univariate tests. Numbers in bold indicates significant tests at the level of $P \leq 0.05$. Significance level: * = $0.01 < P \leq 0.05$, ** = $0.001 < P \leq 0.01$; *** = $P \leq 0.001$.

Source of variation	Wilks´ Λ			Chironomids	Macro invertebrates	Cladocerans	Copepodes
	df	F	df				
cannibal	4, 9	0.41	1, 12	1.65	0.38	0.02	0.31
refuge	8, 12	0.97	2, 9	1.69	0.21	0.23	0.59

Resources

There was an overall higher biomass of the littoral macro invertebrate resource in the absence of cannibalistic char, using MANOVA for the analysis with presence or absence of cannibalistic char as factor (Tab. 1) (Fig. 4). However, neither of the variables, chironomids and other macro invertebrates, could alone account for the effect although there was a strong tendency (p = 0.06) for higher density in other invertebrates when cannibalistic char was absent. Refuge availability had no effect on macro invertebrate biomass, in the presence of cannibals (Tab. 1).

In addition, fish density in cannibal treatments at the end of the experiment was not related to macro invertebrate biomass (Pearson´s correlation, chironomids, r = -0.06, p = 0.84, other macro invertebrates, r = 0.251, p = 0.39), and neither was growth (Pearson´s correlation, other invertebrates r = -0.003 p = 0.993, chironomids, r = -0.185 p = 0.545).

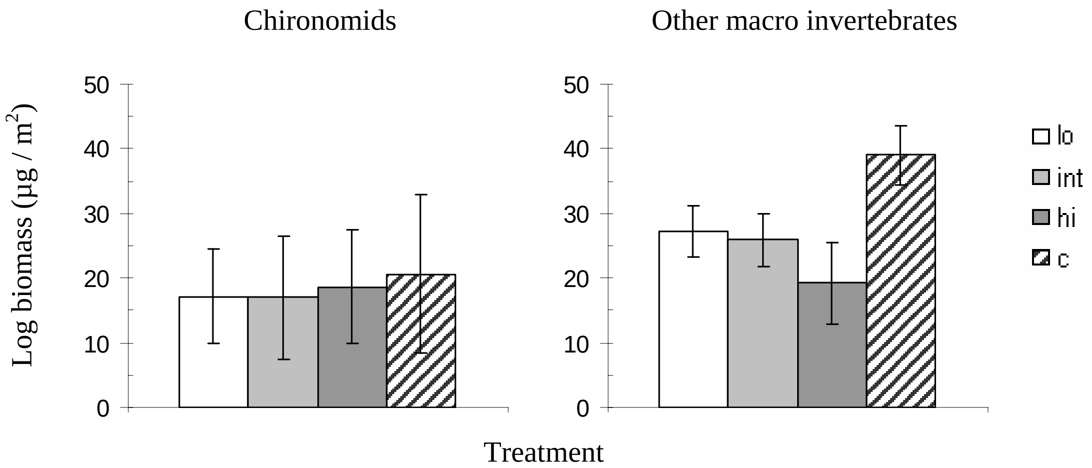

Figure 4. Biomass (µg/m^2 ± 1 SE) of macro invertebrate groups at the end of the experiment for the different treatments.

Table 1. MANOVA (F-values) of the effect of cannibal presence and refuge availability on the diet of YOY char and the following univariate tests. Numbers in bold indicates significant tests at the level of $P \leq 0.05$. Significance level: * = $0.01 < P \leq 0.05$, ** = $0.001 < P \leq 0.01$; *** = $P \leq 0.001$.

Source of variation	Wilks´ Λ			Chironomids	Other invertebrates
	df	F	df	F	
cannibal	2, 11	**4.67***	1, 11	0.09	4.32 (p=0.06)
refuge	4, 16	2.32	2, 9	0.03	0.79

Biomass of cladocerans was positively affected by the presence of cannibalistic char over time (Fig. 5) (Tab. 2) (data analysed with repeated-measures ANOVA with treatment, presence or absence of cannibalistic char, and habitat, pelagic or littoral, as factors). Copepod biomass was not affected by cannibal presence, instead there was a difference over time in biomass between habitats with a higher end biomass in the littoral habitat (Fig. 5) (Tab. 2).

Analysing only for the effect of refuge availability on littoral zooplankton biomasses in presence of cannibals, repeated-measures ANOVA with refuge availability as factor was used. The intermediate refuge treatment had a lower biomass of cladocerans over time than the low treatment (Tukey posthoc, p = 0.03) and a tendency for lower biomass than the high refuge treatment (Tukey posthoc, p = 0.07) (Fig. 5) (Tab. 2).

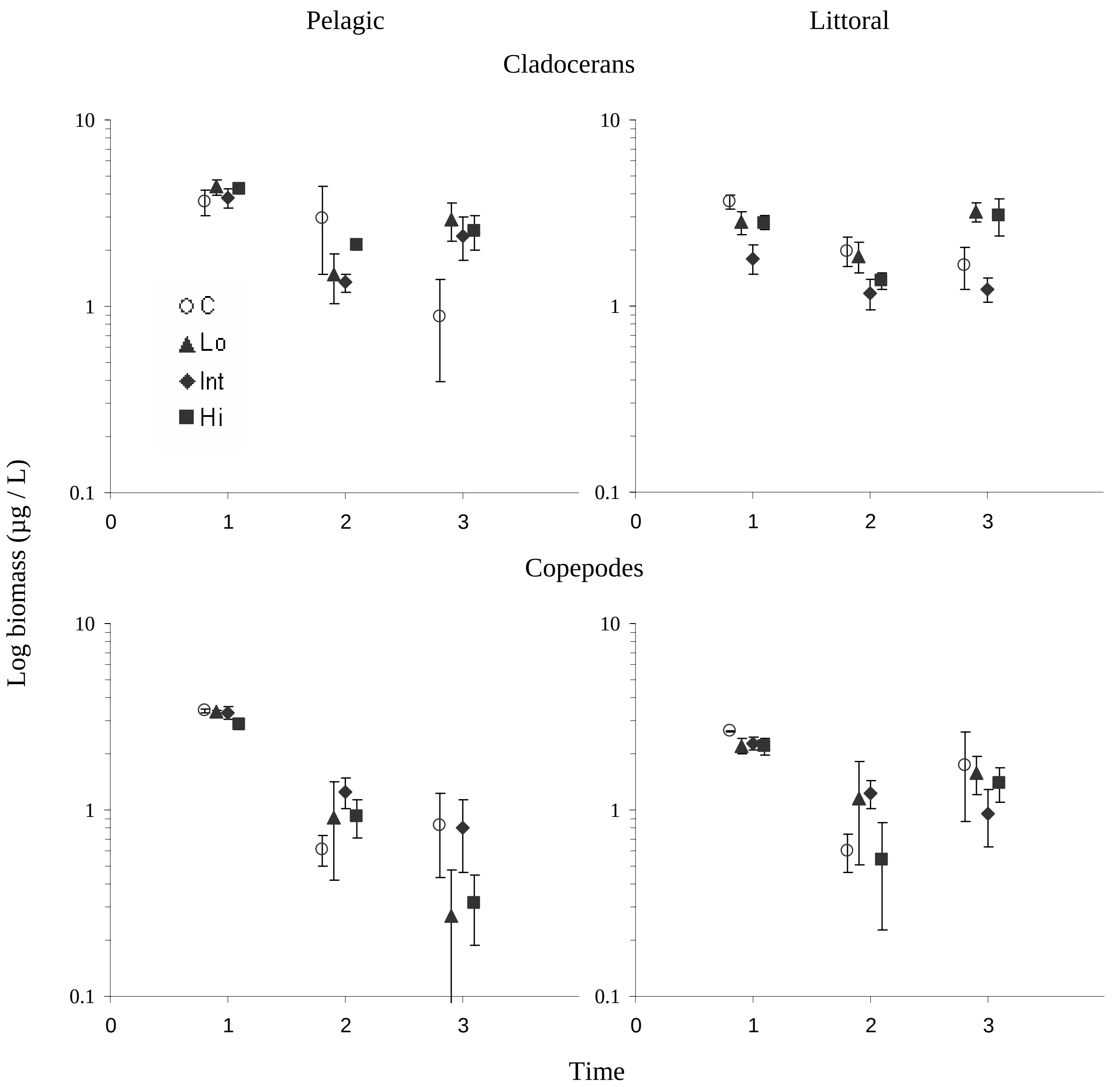

Figure 5. Dry weight (µg/L ± 1 SE) of zooplankton in pelagic and littoral samples over time for the different treatments. Numbers on x-axis represent sampling occasions from start (1), in the middle (2) at the end of the experiment (3).

Table 2. Repeated-measure ANOVA (F-values) of the effects of cannibal presence, habitat and refuge availability on zooplankton biomasses. Numbers in bold indicates significant tests at the level of $P \leq 0.05$. Significance level: * = $0.01 < P \leq 0.05$, ** = $0.001 < P \leq 0.01$; *** = $P \leq 0.001$.

Source of variation		Cladocerans	Copepodes
Test for cannibal effect and habitat differences	df	F	
time	2, 48	**16.66*** **	**74.90*** **
time x cannibal	2, 48	**6.94** **	2.91 (p=0.064)
time x habitat	2, 48	2.01	**11.33*** **
time x cannibal x habitat	2, 48	2.16	0.03
cannibal	1, 24	0.004	0.20
habitat	1, 24	1.21	0.00
cannibal x habitat	1, 24	0.80	0.05
Test for refuge effects			
time	2, 18	**13.24*** **	**20.78*** **
time x refuge	4, 18	2.46	1.55
refuge	2, 9	**5.53***	2.71

Behaviour

There was a striking difference in habitat use of YOY char between enclosures with and without cannibals throughout the experiment, evident by the significant interaction term cannibal x treatment (Fig. 6, Tab. 3). In the treatments without cannibals, YOY char were observed only occasionally in the refuge area and mainly in the open water habitat (Fig. 6). Char in treatments with cannibals had the opposite behavioural pattern, mostly observed in the refuge area (Fig. 6). Furthermore, 92% of the observations of YOY char in the intermediate refuge treatment were done in the artificial refuge, indicating the preference of the additional artificial refuge in comparison to the natural near shore vegetation refuge.

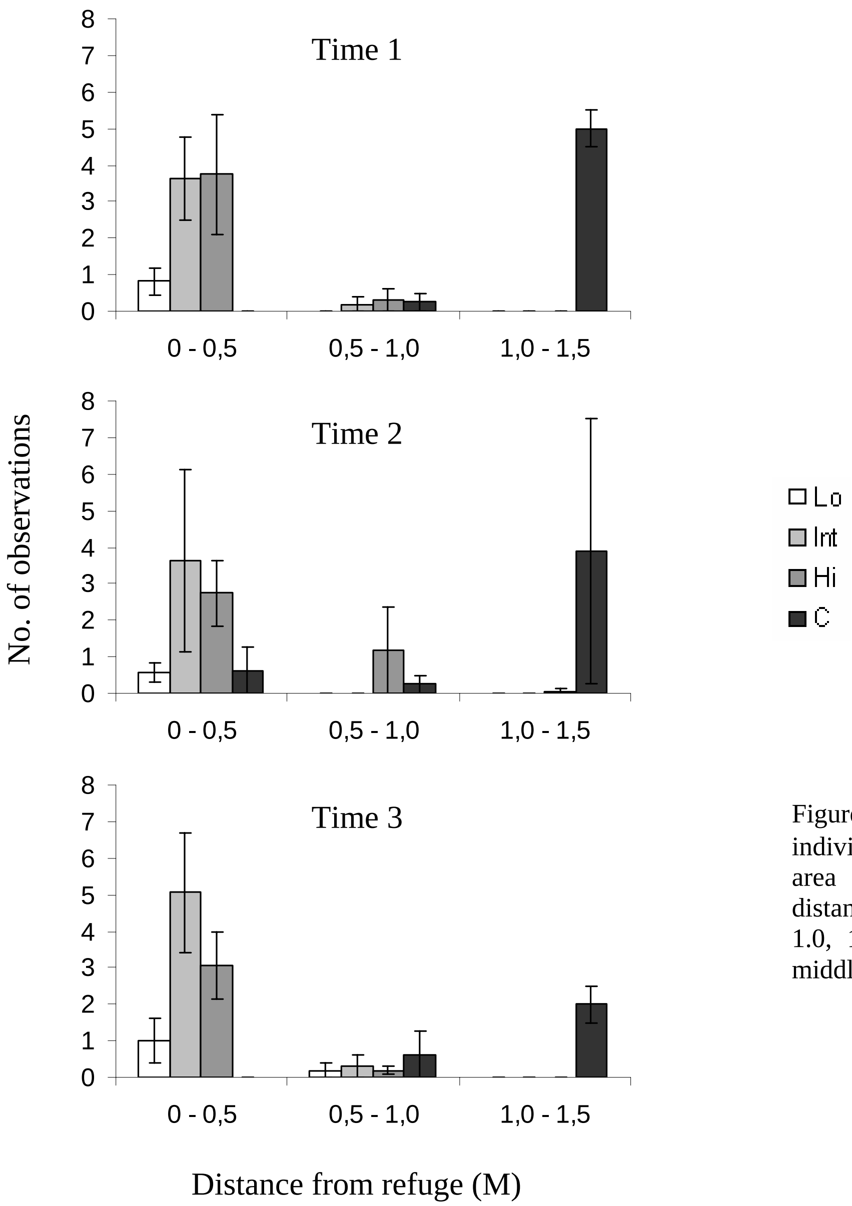

Figure 6. Number of observed individuals (± 1 SE) in the refuge area (0-0.5 m) and at different distances from the refuge area (0.5-1.0, 1.0-1.5 m), at the beginning, middle and end of the experiment.

Table 3. Repeated measures ANOVA (F-values) of the effect of cannibal presence on YOY char behaviour, number of observed individuals.

Source of variation		Observations
Test for cannibal and habitat effects	df	F
time	2, 72	0.75
time x cannibal	2, 72	1.46
time x distance	4, 72	1.59
time x cannibal x distance	4, 72	1.63
Cannibal	1, 36	0.53
Distance	2, 36	2.07
cannibal x distance	2, 36	**7.88** **

Discussion

Refuge availability and survival

I predicted that increasing refuge availability would increase survival of YOY Arctic char, and correspondingly my results also suggested that survival was dependent on refuge availability. YOY char in the natural low density refuge treatment were heavily affected by predation compared to treatments with additional refuges, where YOY char had approximately two times higher survival rates. Since the initial density of YOY char were the same between treatments but the amount of available refuge differed, an increase in fish density within the refuge area with decreasing refuge availability was expected, if YOY char increased their use of refuges in response to the presence of cannibals. The increased use of the refuge area was supported by the behavioural study, suggesting that fish density in refuges would be dependent of the size of the refuge area. Steele & Forrester (2004) suggested that increasing refuge availability increases survival and it has also been argued that there is a threshold density of individuals where some individuals have to live outside the refuge (Connell 1970, Butler and Herrnkind 1997). Increasing refuge availability would then decrease mortality from predation as suggested by the results in this study.

The lower survival rate observed in the low natural refuge treatment compared to the intermediate and high density refuge treatments could in part be the effect of qualitative differences to provide shelter from predation between the natural near shore vegetation habitat in the pond and the additional artificial refuge. Consequently, the similar survival of intermediate and high refuge treatments may then be the combined effects of the relatively high quality of the additional artificial refuge and the short time scale of the experiment, rather then the differences in density of available refuges in those treatments. In addition, the natural refuge still available in the intermediate treatment provided additional shelter to the available artificial refuge, making the absolute difference in refuge availability smaller between the intermediate and high refuge treatments. In the long run, however, one could expect the differences in survival between different amounts of artificial refuges to become more evident as density dependent resource depletion also could be expected to increase with time. For example, Biro et al. (2003c) have by manipulating densities of young Rainbow trout (*Oncorhynchus mykiss*) at the lake scale shown that density dependent mortality is mediated by foraging activity. Mortality of rainbow trout were higher in high density populations, were activity and the use of risky habitats of age-0 trout were higher.

The results from this study also suggest that the natural near shore habitat with vegetation provided little protection from predation, compared to the artificial refuges. The more three dimensionally complex artificial refuge resembles more a refuge habitat consisting of rocks, boulders and stones. In addition, Byström et al. (2004) concluded that survival of YOY char during summer is high mainly as an effect of low resource limitation and restricted habitat use to the very near shore habitat consisting of boulders, rocks and stones. The results from this study suggests that in lakes were near shore habitat is dominated by vegetation survival of YOY char may be lower than in lakes where the near shore habitat is dominated by rocks boulders and stones. Hence, quality of refuges appears to have strong effects on survival of small char and overall the result from this study then suggests that both availability and quality of the refuge are important factors affecting mortality rates in populations.

Growth and resource levels

I expected increasing refuge availability to increase growth of YOY arctic char in the presence of cannibals. I also expected that resource densities adjacent to the refuge area would be lower compared to the open water, due to increased refuge use by YOY char in the presence of cannibals. Growth was negatively affected by the presence of cannibalistic char, but increasing refuge availability did not increase growth rates.

The observed lower growth of YOY char in presence of cannibals could be an effect of that cannibals induces a change in habitat use of YOY char, and consequently high densities of sheltering individuals causes resource depletion which limits growth in the refuge habitat. In addition, the use of the refuge habitat causes a lost of foraging opportunities in the open pelagic and benthic habitat which further increases the likelyhood for resource limitation in YOY char. Cladoceran biomass, for instance, was higher in the pelagic samples of cannibal treatments compared to treatments without cannibals, indicating that YOY char utilized the pelagic resource in the absence of cannibals. The patterns in zooplankton and macro invertebrate biomasses suggested that habitat use and density of YOY char in the refuge area affected the resource levels. Macro invertebrate fauna was lower in the refuge area of cannibal treatments compared to treatments without cannibals, further supporting the negative effect on refuge resources by increased fish density within the refuge area. Since the density of fish within the refuge area was twice as high in the intermediate refuge treatment as in the high treatment. There was also a density dependent depletion of cladoceran resources, indicated by the additional test of the cladoceran biomass in littoral samples of the control, intermediate and high refuge treatments, with a lower biomass of the intermediate treatment (Repeated-measures ANOVA, refuge x time effect, $F_{4,14} = 3.93$, $p = 0.024$, One-way ANOVA, refuge effect, $F_{2,7} = 5.54$, $p = 0.036$) (Fig. 4). Although resources were negatively affected by higher fish density, growth and survival of YOY char in cannibal treatments were positively related. Indicating that the density dependent depletion of resources observed was not the major factor affecting the growth of YOY char. Diets of YOY char could neither explain the observed lower growth caused by cannibal presence, as there was no difference in the diet or any indication of specific resources being utilized in the absence of cannibals. Instead, the decreased growth of YOY char in the presence of cannibals is more likely to be a consequence of decreased time spent foraging under the risk of predation.

In response to the presence of cannibals, YOY char used the refuge area to minimize the risk of predation, and also activity was decreased in the presence of cannibals (pers. observations). In combination with the positive correlation between growth and survival and the negative effect of predator presence on growth, predation risk is suggested to have stronger effects on growth in this study rather than actual resource competition in the refuge habitat. The evidence of reduced growth as a behaviourally mediated effect from predator presence is also common in the literature (Sih 1982, Werner and Gilliam 1984, Lima and Dill 1990, Houston et al. 1993, Werner and Anholt 1993).

Conclusion

In summary, the results of this study shows that survival of YOY char increased with increasing refuge availability, contrasting to growth which was unaffected by increasing refuge availability but still negatively affected by predation risk. Predation risk also restricted the habitat use of YOY char to the structurally complex near shore habitat, suggesting a change in habitat use by YOY char in response to predation. Results also show a density dependent resource depletion induced by refuge availability and habitat use of YOY char in the presence of cannibals. However, both growth and survival were unaffected by resource availability, suggesting predation and not resource competition to be the key factor regulating growth and mortality in YOY char.

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